

ments on provenance is that seed of local origin is the best type to be planted in a given region. However, as Schreiner (1937) has pointed out, there are exceptions to this general rule and for this reason more complete data on seed origin will be of invaluable aid in any program of forest genetics. It is well known that among trees of a given area there may be differences in rate of growth, form, and resistance to disease or adverse environmental conditions. For this reason it is desirable from the point of view of forest genetics to make progeny tests from individual trees in order that the very best trees may be selected for hybridizing experiments.

Simultaneously with investigations of seed origin and progeny tests actual hybridizing among forest tree genera, species, and varieties must play an important part in any program of forest tree improvement. It is only in comparatively recent years that this phase of the problem has been undertaken on a large scale. However, for over a century foresters have considered the production of entirely new types of forest trees by means of hybridization. Klotzsch (1854) was apparently the first investigator to report hybridizing experiments in forest trees. In 1845 he produced artificial hybrids in pine, oak, elm, and alder and noted remarkable vigor in the hybrids. In 1891 Luther Burbank is reported to have produced the remarkable Paradox walnut, a hybrid between *Juglans regia* and *J. californica*. It was not until the early part of the 20th century that Augustine Henry gave new impetus to the idea of breeding forest trees. In 1914 Henry reported on artificial hybridization in ash, elm, larch, poplar, beech, and oak.

Since 1914 many programs of forest tree breeding have been initiated in this country as well as in Europe. Worthy of mention among these more recent attempts are the chestnut breeding experiments endeavoring to obtain a blight resistant type, the poplar hybridization work of the Oxford Paper Company, and the work of the Institute of Forest Genetics in California which was undertaken in 1925.

In planning a program of forest tree improvement it is well to consider carefully just what improvements will be of most value. Increased vigor and rate of growth are commonly found in first generation species hybrids. This fact immediately suggests that rapidity of growth would be one of the primary aims in producing forest tree hybrids. However, there are other facts which must be taken into consideration. If a particular forest tree is used exclusively for timber production then the quality of the timber in the hybrid is of utmost importance. Generally speaking, timber from the more rapid growing conifers is somewhat weaker and inferior to the timber from slower growing trees. On the

other hand, in certain of the best hardwood timber trees, rapidity of growth tends to strengthen and improve the quality of the timber (Henry, 1914). Certain forest trees such as spruce and poplar are used largely for pulp and plastics. In such cases the strength and quality of the wood is of secondary importance. The primary aim would be the production of a rapid growing hybrid from which a merchantable crop could be obtained in a shorter period of time.

Perhaps of equal importance in hybrid forest trees is the question of disease resistance. Plant breeders dealing with agricultural crops have always found disease resistance of primary importance. In order to realize that disease resistance is important in forestry it is only necessary to recall the fate of the American chestnut. Foresters are aware of this fact and intensive breeding experiments have been in progress in an attempt to produce a chestnut which is resistant to the chestnut blight and still retains all the desirable qualities of a good timber tree.

The importance of seed origin studies and hybridization have been discussed briefly above. There is another phase of the problem which must not be neglected. Seed from first generation hybrids does not breed true. Therefore, in order to perpetuate any desirable hybrid, vegetative reproduction must be used. If vegetative reproduction can be used successfully the hybrids may be multiplied rapidly without waiting for the trees to mature and there is no danger of losing any of the first generation vigor or other advantageous characters.

Vegetative propagation of most conifers and many of the commonest hardwood trees has been considered difficult (Thimann and Delisle, 1939). Extensive studies on rooting ability reveal the fact that with the aid of optimal concentrations of auxin and proper age of the trees from which cuttings are taken, most of the difficult species can be rooted. Cuttings from young white pine trees, 3 or 4 years old, root most successfully. However, not many cuttings can be obtained from a single tree of such an age and vegetative propagation is not yet possible on a commercially profitable scale.

The recent discovery that colchicine may be used to double the chromosome number in plants makes this chemical a valuable aid to plant breeders. In cases where a species hybrid is sterile, the use of colchicine may double the chromosome number to produce a true breeding amphidiploid with complete fertility. Colchicine may be of further value in forestry by producing polyploid forms of existing forest tree types. The polyploid forms are often more vigorous than the diploid forms from which they were derived.

A study of natural hybridization is of value in showing the degree of

species hybridization in various genera. The occurrence of natural interspecific hybrids in forest trees depends upon the realization of three conditions—that flowering times of the species coincide, that the genetic relationships between the species concerned be such as to permit crossing, and that the geographic distribution of the species coincide to some extent. These conditions are sufficient to account for natural hybrids in the case of dioecious species, however, isolation mechanisms such as self-sterility, protandry, and protogyny are required in the case of monoecious species. Protandry and protogyny are widespread in forest tree genera (Larsen, 1937; East, 1940). In regard to self-sterility Larsen has this to say, "The majority of our forest trees should not be classified for purposes of breeding with the absolutely self-sterile plants but ought rather to be included among those plants which normally are cross-pollinated but can by artificial means be rendered self-pollinated."

Due to the widespread occurrence of protandry and protogyny and the occasional occurrence of dioecious species in forest trees, natural interspecific hybrids are common. Among these the London plane, *Platanus acerifolia* (Ait.) Willd., the cricket-bat willow, *Salix alba* L. var. *calva* G. F. W. Mey., and the common linden, *Tilia europaea* L., are natural hybrids of considerable economic importance. *Platanus acerifolia*, according to Henry and Flood (1919), originated in the Oxford Botanic Garden about 1670 as the result of a cross between *P. occidentalis* L. and *P. orientalis* L. This tree is extensively planted as a shade tree in localities where neither parent can survive. *Tilia europaea* is widely planted and is valuable as a hardy shade tree. It is the hybrid *T. cordata* Mill. \times *T. platyphyllos* Scop. *Salix alba* var. *calva* is recognized by Henry (1914) as a hybrid between *S. alba* and *S. fragilis* L. It probably originated at Norfolk, England, about 1700 and is used extensively in the manufacture of cricket-bats. However, Wilkinson (1941), on the basis of a cytological investigation of *S. alba*, *S. fragilis*, their varieties and hybrids concludes that *S. alba* var. *coerulea* (= *S. alba* var. *calva*) is a variety of *S. alba* and not a hybrid.

The occurrence of natural hybrids in the genera of forest trees and the success of artificial species hybrids provides some information of value in planning a breeding program, and at the same time indicates the relationships of the species in the various genera. The chromosome numbers also are of interest in respect to crossing diploid and polyploid species, and provide some indication of the probable success of the artificial production of polyploids.

The data on natural and artificial interspecific hybrids in sixteen genera of local importance are shown in table 1. Of these genera only

one, *Fagus* L., has no interspecific hybrids reported. The table is based for the most part on the list of interspecific hybrids in tree genera published by Johnson (1939). Some additions and changes have been made. Crosses using varieties of species or hybrids which have not been assigned a specific name as parents have been omitted. It is unfortunate that in the original hybrid lists, the name of the authority for the species name was often omitted. Nevertheless, an attempt has been made to bring these lists into agreement with the system of naming used by Rehder (1940). The same authority was used for approximate number of species within the genera and for division of the genera into subgenera, sections and series. Chromosome numbers were taken from the lists of Tischler (1927, 1931, 1936, 1938) and from various later publications (Peto, 1938; Dillewijn, 1940; Duffield, 1940). In the case of *Populus* and *Catalpa* some chromosome numbers were taken from the work of Smith (unpublished).

TABLE I

| GENUS | SPECIES IN GENUS | CHROMOSOME NUMBER | NATURAL HYBRIDS | ARTIFICIAL HYBRIDS | SPECIES USED IN CROSSES |
|----------|---------------------|-----------------------------|--------------------|-----------------------|-------------------------------|
| ABIES | 40 | 12 | 2 | 1 | 5 |
| ACER | 115 | 13, 26, $\frac{39}{2}$, 52 | 10 | 1 | 11 |
| BETULA | 40 | 14, 28, 35, 42 | 11 | 11 | 14 |
| CARYA | 20 | 16, 32 | 7 | 0 | 7 |
| CASTANEA | 10 | 12 | 6 | 10 | 8 |
| CATALPA | 10 | 20 | 1 | 1 | 2 |
| FAGUS | 10 | 12 | 0 | 0 | 0 |
| FRAXINUS | 65 | 23, 69 | 0 | 4 | 4 |
| JUGLANS | 15 | 16 | 7 | 8 | 6 |
| LARIX | 10 | 12 | 6 | 4 | 9 |
| PICEA | 40 | 12 | 4 | 3 | 6 |
| PINUS | 80 | 12 | 11 | 7 | 20 |
| POPULUS | 30 | 19, $\frac{57}{2}$ | 12 | 81 | 27 |
| QUERCUS | 200 | 12 | 60 | 2 | 50 |
| TILIA | 30 | 41, 82 | 9 | 0 | 9 |
| ULMUS | 18 | 14, 28 | 3 | 3 | 7 |

The genus *Acer* L. is divided into fourteen sections. The hybrids listed are the result of crosses between species within the section *Platanoidea* Pax and the section *Spicata* Pax, and crosses between species belonging to different sections as follows: *Platanoidea* × *Campestris* Pax, *Campestris* × *Spicata*, *Spicata* × *Macrantha* Pax. Most of the crosses occur between the sections *Campestris* and *Spicata* with only one cross between the sections *Spicata* and *Macrantha*. Chromosome counts up to this time, based on the examination of some seventeen species, show a polyploid series based on a reduced number of $n = 13$. Meurman (1933) finds that, on the basis of secondary association of chromosomes in *A. platanoides* L., the basic ancestral chromosome number is $n = 12$. The genus is self-fertile as far as is known (East, 1940). The artificial cross *A. rubrum* L. × *A. saccharinum* L. has been reported by Freeman (1941). Both parent species belong to the section *Rubra* Pax.

The genus *Fraxinus* L. is divided into sections and subsections. Johnson (1939) does not list any hybrids in this genus, but Henry (1914) reports seedlings from four crosses. Some of these were seen by Anderson in 1934 (Anderson and Whelden, 1936), at which time they were vigorous young trees. All four crosses occur between species within the same section of the genus, *Fraxinaster* DC. Two are crosses within the subsection *Melioides* Endl., and two are crosses between the subsections *Melioides* and *Bumelioides* Engl. The work of Anderson and Turrill (1938) indicates that natural hybridization does take place in the case of *F. oxycarpa* Willd. and *F. Pallisae* Wilmott. Of the six species for which chromosome numbers have been determined, five have the reduced number $n = 23$ while one species has $n = 69$. East (1940) reports no cases of self-sterility in this genus.

Quercus L. is divided into three subgenera, the last of which is redivided into six sections. Hybridization in this genus seems to be limited to species which belong to the same subgenus (Trelease, 1924; Johnson, 1939). In the case of the subgenus *Lepidobalanus* Endl., crossing occurs between species belonging to different sections, although most of this is limited to the section *Prinus* Loud. On the basis of chromosome counts of forty-six species, the genus has a chromosome number of $n = 12$.

The Fagales and especially the genera *Betula* L., *Fagus* L., *Castanea* Mill., and *Quercus* are very protandrous, so much so that isolated trees bear almost no fruit, but there seems to be no difficulty in getting selfed seed by artificial pollination. All are self-fertile (East, 1940). The chromosome number in *Fagus* is 12, in *Castanea* 12, in *Betula* the base

number is 14 but a polyploid series of 14, 28, 35, and 42 exists. These reduced numbers are founded on chromosome counts of one, two, and twenty-five species and varieties respectively.

The genus *Populus* L. is divided into five sections, *Leuce* Duby, *Leucoides* Spach, *Tacamahaca* Spach, *Aegeiros* Duby, and *Turanga* Bge. Species hybrids within and between the sections *Leuce*, *Tacamahaca* and *Aegeiros* are known, although those within and between the latter two sections are the most common. Johnson (1939) states that there appears to be little limitation to species hybridization in this genus. Heimburger (1940) sees a definite limitation to species hybridization based on genetic affinities which cause crossing to follow a series similar to the series aspens — silver poplars — cottonwoods — balsam poplars. Thus far no crosses involving species belonging to the sections *Leucoides* and *Turanga* have been reported, but it seems to be possible to make any desired cross between and within the remaining three sections. Chromosome counts based on the investigation of thirty-six species and varieties of *Populus* show the reduced number in this genus to be 19. Occasional triploid forms are known within the section *Leuce*. One tetraploid form has been reported, but subsequent investigations show that $n = 19$ is the common haploid number for this species, although it is conceivable that it does exist in the tetraploid form. Dillewijn (1940), on the basis of secondary association of chromosomes at pre-meiotic metaphase of the meiotic divisions, concludes that $n = 8$ is the real base number and that the genus is a secondary polyploid. The genus is dioecious as a rule. When monoecious trees appear they are self-fertile (East, 1940).

Ulmus L. is divided into five sections. The reported hybrids occur between species in the section *Madocarpus* Dum. There is one exception, the probable hybrid which Klotzsch produced in 1845 and reported as *U. campestre* \times *U. effusa*. The parent species, if correctly given, here belong to the sections *Madocarpus* and *Blepharocarpus* Dum. respectively. Chromosome counts of thirteen species show the reduced number to be 14, with one tetraploid species. As far as is known all species within this genus are self-fertile but there is marked protogyny (East, 1940).

The genus *Carya* Nutt. has a haploid number of $n = 16$, with some tetraploid species. These conclusions are based on an investigation of seven species. *Juglans* L. also has a reduced number of 16 based on counts of seven species. East (1940) has investigated all the common species of *Juglans* and *Carya* and finds them to be self-fertile, though tending to be protandrous.

Tilia L. has one or more species known to be self-fertile, while a considerable amount of protandry is known in the Tiliaceae. In *Tilia*, chromosome counts on 12 species show the basic haploid number to be $n = 41$, with both diploids and tetraploids known in the genus. *Catalpa* Scop., of the Bignoniaceae, is a self-fertile genus (East, 1940). The haploid chromosome number in the genus is 20 based on the examination of three species.

The genus *Picea* A. Dietr. is divided into three sections. The hybrids listed occur as the result of crosses both between and within sections, with more occurring between than within the sections.

Pinus L. is divided into two subgenera, three sections, and ten series. With few exceptions hybrids occur between species belonging to the same series. There are no reported hybrids from crosses of species belonging to different sections or subgenera. The parents of most of the reported hybrids belong to the subgenus *Diploxylon* Koehne, section *Pinaster* Endl. Two hybrids are reported between species belonging to the subgenus *Haploxylon* Koehne, section *Cembra* Spach.

In the genera of the Pinaceae considered here all the species thus far investigated have the reduced chromosome number of $n = 12$. This number is based on the examination of five, six, five, and twenty-one species respectively for the genera *Abies* Mill., *Larix* Mill., *Picea*, and *Pinus*. They are thought to be self-fertile though normally cross-pollinated (Larsen, 1937).

The hybridization work at the Arnold Arboretum has been limited largely to *Populus*, *Betula* and *Pinus*. These genera are of value in reforestation projects particularly where the trees are to be used as a source of cellulose. The incidence of both natural and artificial hybrids shows that interspecific hybridization in these genera occurs readily.

The technique employed in the hybridization of forest trees is essentially that employed in the breeding of any flowering plants. Schreiner (1938), among others, has published on methods of tree hybridization. However, each genus requires modifications of the general technique.

Yanchevsky (1904) seems to have been the first to use a method by which flowering branches of *Salix* were brought into the greenhouse, flowered, and seed matured. Wettstein (1933) employed this method in *Populus*. The authors have also used this method in this genus, where it has proved most successful in the case of species belonging to the section *Leuce*. Crosses in other sections of the genus were more successful when made on the trees. Since pollen from all species of *Populus* may be forced in the greenhouse, the advantage of being able to overcome natural differences in blooming time is not lost when crossing must be done in the field.

The forcing of pollen in the greenhouse may be used successfully in the case of *Betula*. Here sausage tubing may be used in place of the usual glassine bags when it is desired to cover a large number of small flowers on one branch. The best results were obtained when the ends of the tube were plugged with cotton wool, thus allowing for some aëration.

Ulmus may be treated in a manner similar to *Populus* in that branches may be brought into the greenhouse and flowered, crosses made, and seed matured. The perfect flowers of *Ulmus* are small and difficult to emasculate. However, since the genus is strongly protogynous, crosses may be made without emasculation. This method was used successfully by the authors in certain crosses made in the greenhouses of the Arnold Arboretum in the spring of 1938. As the knowledge of flowering habits in forest trees grows, increasing use of protandry, protogyny, and self-sterility will simplify hybridization techniques.

Isolated trees of dioecious species or of monoecious species which are strongly protandrous or protogynous may be used as a source of hybrid seed providing that trees of other species in the genus are flowering in the neighborhood. Accurate records on the blooming times of all trees in the vicinity will aid in determining what the male parents probably are.

In the genus *Quercus* there are a large number of natural hybrids but very few reports of artificial hybrids. This must indicate that proper techniques have not yet been developed for this group. A similar lack of technique probably accounts for the failure to obtain artificial hybrids in the genus *Acer*.

There is some evidence that an overabundance of pollen on the stigmas of female flowers in *Juglans* and *Carya* prevents crosses from being successful. Special techniques are needed in order that small amounts of pollen can be used when dealing with these groups.

Very often a cross may yield a good set of seed but the seed may not germinate. In many cases this failure of germination may be due to an upset in the ratio of embryo size to endosperm size. This difficulty may be overcome by making use of the technique of embryo culture. If the embryo is removed from the seed at the critical stage and placed on nutrient media a healthy and mature plant may be obtained where ordinary methods of germination fail.

Crosses between species of *Pinus* and other genera of conifers have been made, but the resulting seedlings are not large enough for critical study. The work on *Pinus* has been confined to the white pine species.

The hybrids in the genus *Populus* are grown in nursery plots and are cut back severely to induce an abundance of lateral sprouts from which

cuttings can be obtained. These cuttings will provide the trees to be tested at the Harvard Forest in comparison with the parental species or with hybrids of known value.

The authors have attempted a number of interspecific crosses in the genera *Abies*, *Betula*, *Carya*, *Catalpa*, *Fagus*, *Fraxinus*, *Juglans*, *Picea*, *Pinus*, *Populus*, *Quercus*, and *Ulmus* during the past three years. This work has been done under the Maria Moors Cabot Foundation for Botanical Research on trees growing in the Arnold Arboretum of Harvard University. The following list of crosses represents part of the work done in the years 1938 and 1939. The resulting trees have been tentatively identified as hybrids. No attempt has as yet been made to compare the vigor of these young trees with that of the parent trees or with other hybrids, but the cross *Ulmus Wilsoniana* Schneid. \times *U. japonica* (Rehd.) Sarg. seems to be more vigorous and more resistant to insect attack than is *U. japonica*. Among the hybrids in the genus *Populus*, those crosses using the species *P. Maximowiczii* Henry as the female parent seem to be the most promising.

Betula L.

- B. mandshurica* (Reg.) Nakai var. *japonica* (Miq.) Rehd. \times *B. lenta* L.
B. mandshurica (Reg.) Nakai var. *japonica* (Miq.) Rehd. \times *B. Maximowicziana* Reg.
B. mandshurica (Reg.) Nakai var. *japonica* (Miq.) Rehd. \times *B. nigra* L.
B. mandshurica (Reg.) Nakai var. *japonica* (Miq.) Rehd. \times *B. populifolia* Marsh.
B. mandshurica (Reg.) Nakai var. *japonica* (Miq.) Rehd. \times *B. papyrifera* Marsh.
B. lutea Michx. \times *B. lenta* L.
B. papyrifera Marsh. var. *kenaica* (Evans) Henry \times *B. mandshurica* (Reg.) Nakai var. *japonica* (Miq.) Rehd.
B. populifolia Marsh. \times *B. lenta* L.
B. populifolia Marsh. \times *B. papyrifera* Marsh.

Populus L.

- P. alba* L. var. *nivea* Ait. \times *P. deltoides* Marsh.
P. alba L. var. *nivea* Ait. \times *P. adenopoda* Maxim.
P. canescens (Ait.) Sm. \times *P. alba* L. diploid
P. canescens (Ait.) Sm. \times *P. alba* L. triploid
P. canescens (Ait.) Sm. \times *P. deltoides* Marsh.
P. canescens (Ait.) Sm. \times *P. tomentosa* Carr.
P. cathayana Rehd. \times *P. deltoides* Marsh.
P. cathayana Rehd. \times *P. laurifolia* Ledeb.
P. deltoides Marsh. \times *P. acuminata* Rydb.
P. deltoides Marsh. \times \times *P. canadensis* Moench.
P. deltoides Marsh. \times *P. nigra* L.
P. Maximowiczii Henry \times *P. deltoides* Marsh.

- P. Maximowiczii* Henry × *P. laurifolia* Ledeb.
P. Maximowiczii Henry × *P. nigra* L.
P. Maximowiczii Henry × *P. tomentosa* Carr.
P. nigra L. var. *italica* Muenchh. × × *P. canadensis* Moench.
P. Sargentii Dode × *P. acuminata* Rydb.
P. Sargentii Dode × *P. deltoides* Marsh.
P. Tacamahaca Mill. × × *P. canadensis* Moench.
P. Tacamahaca Mill. × *P. deltoides* Marsh.
P. Tacamahaca Mill. × *P. nigra* L.
P. Tacamahaca Mill. × *P. nigra* L. var. *italica* Muenchh.
P. Tacamahaca Mill. × *P. Simonii* Carr.
P. tomentosa Carr. × *P. adenopoda* Maxim.
P. tomentosa Carr. × *P. alba* L. diploid
P. tomentosa Carr. × *P. alba* L. triploid

Ulmus L.

- × *U. hollandica* Mill. × *U. japonica* (Rehd.) Sarg.
U. Wilsoniana Schneid. × *U. japonica* (Rehd.) Sarg.

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A NOTE ON THE DATES OF ISSUE OF THE FASCICLES
COMPRISING COSSON'S "ILLUSTRATIONES FLORAE
ATLANTICAE" 1882-1897

E. D. MERRILL

As noted by Stearn* in his comprehensive consideration of the dates of publication of this important two-volume work, the inclusive dates for volume one are 1882-1890 and for volume two 1893-1897, publication thus extending over a period of fifteen years. The only reason for the publication of this note is the fact that Stearns saw no fascicle covers, which carry the dates of publication and the inclusive pages and plates of each fascicle. A second set of the work was recently acquired by the Arnold Arboretum, this fortunately in its original fascicle covers. In our bound library set the fascicle covers are missing, and this seems to be the case in most libraries; the chief reason for their non-preservation, other than the earlier and unfortunately common practice of discarding such covers, is probably due to the fact that the covers are of rather heavy bristol board and thus were not adaptable to binding. The following data are taken directly from the original fascicle covers:

VOLUME I

| | FASCICLE COVER DATES | STEARNS' DATES |
|---|-------------------------|-------------------|
| Fasc. I, pp. 1-36, <i>t.</i> 1-25. | Sept., 1882 | Oct. 10, 1882 |
| Fasc. II, pp. 37-72, <i>t.</i> 26-50. | Aug., 1884 | August, 1884 |
| Fasc. III, pp. 73-120, <i>t.</i> 51-73. | Dec., 1888 | Jan.-Feb., 1889 |
| Fasc. IV, pp. 121-159, <i>t.</i> 74-98. | Oct., 1890 | Jan. 10, 1891 |

VOLUME II

| | | |
|--|------------|-----------------|
| Fasc. V, pp. 7-42, <i>t.</i> 99-123. | Feb., 1892 | April, 1892 |
| Fasc. VI, pp. 43-82, <i>t.</i> 124-148. | Nov., 1893 | Nov.-Dec., 1893 |
| Fasc. VII, pp. 1-6, 83-125, <i>t.</i> 149-175. | May, 1897 | July-Aug., 1897 |

*STEARNS, W. T. Dates of publication of some floras of north-west Africa: Desfontaines' "Flora Atlantica," Cosson's "Compendium," Cosson and Baratte's "Illustrationes," Battander and Trabut's "Flore." Jour. Soc. Bibl. Nat. Hist. 1: 145-150. 1938.